12 Decomposing activity of basidiomycetes in forest litter

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In discussion on the decomposition of forest litter, it is always admitted that basidiomycetes play an important rôle. In general, we cannot yet express this importance by means of a numerical estimate of the proportion of litter materials that they process, and this review will cover work that illustrates their importance in qualitative terms. It will draw on fairly old as well as recent work, for new work on the decomposer basidiomycetes appears at a relatively slow rate.

Mull and mor

In temperate countries the amount of litter reaching the forest floor each year varies widely, with a mean value of about 2 t ha^{-1} dry weight. Decomposition is a long process, and the half-life for the carbon mineralisation of a litter sample may be two years or longer, depending on conditions. In nature the process always involves animals, fungi and bacteria, and we can recognise two very distinctive patterns of decay, leading to very different kinds of soil profile, although there are many intermediate types. In mull, soil animals are active in the fresh litter, and there is a peak of microbial activity later, whereas in mor, the litter is initially unpalatable to animals, so a primary phase of microbial decay precedes attack by animals. In typical mull soils the litter is quickly removed from the soil surface by animals, especially earthworms, so that for most of the year the soil surface is almost bare of litter, being a crumbly mass of worm casts, in which organic and inorganic matter are intimately mixed. The animals divide up the plant matter finely, but they make little impact on macromolecules such as cellulose and lignin; these are incorporated in the soil in casts and faecal pellets, where they become available for attack by micro-organisms. The evidence that the

Table 1. *Total numbers and fresh weights of decomposer agarics collected from permanent plots totalling 300 m² in each of two woodlands in Cumbria, England.* In the period September–November of three successive years, a total of twenty-five visits were made to each site. (From Hering, 1967)

	Mull site		Mor site	
	Number	Fresh weight (g)	Number	Fresh weight (g)
Clitocybe langei sensu Singer			41	30
Collybia peronata			50	139
Cystoderma amianthinum			17	10
Laccaria amethystea			34	43
L. laccata	44	12	352	171
Marasmius epiphyllus	190	2		
M. ramealis	31	1		
Mycena galericulata	28	27	203	210
M. galopus	226	36	292	34
M. metata	171	10		
M. polygramma	24	33		
M. speirea	211	4		
M. sanguinolenta	4	1	14	1
Psathyrella squamosa	4	1	62	85
Total	933	127	1065	723

higher fungi are involved in this process comes from the fact that their fruit bodies emerge from this layer of the soil. Many small toadstools, such as species of *Lepiota* and *Pluteus*, that are described in floras as growing on damp rich soil in woods, may be decomposing this finely divided, buried, material. However, there has been very little detailed study of such fungi to confirm this. Table 1 shows the results of comparable surveys on mull and mor sites in the same region. Mor had a much greater weight of fruit bodies, and comparative equality of numbers was reached only because of the presence on the mull site of very small toadstools such as *Mycena speirea* and *Marasmius epiphyllus*, fruiting on twigs and stalks lying on the soil surface. This material is unpalatable to earthworms, and harbours a distinctive component of the toadstool flora. It seems likely that low fruit-body production is a general feature of mull soils, though they are not often surveyed. On the evidence of fruit bodies – and that is all we have to go on as yet – the rôle of basidiomycetes in mull could be a fairly minor one.

In a mor profile, the litter is not sufficiently palatable to be rapidly

removed by animals, so it lies on the soil surface until it is covered by new litter, and the mineral soil is permanently hidden by a series of organic layers, traditionally described as:

L   intact dead leaves;

F   broken up, but still recognisably composed of leaf pieces;

H   dark, powdery, organic material.

There is a very obvious connection between decomposer basidiomycetes and the F-layer. Often fruit bodies can be seen to be 'rooted' in the F-layer material, with hyphal systems radiating out across the leaf pieces. Mycelial strands are very frequent too, and often show clamp connections, as does the surface mycelium. This in itself does not conclusively show that these organisms are carrying out decomposition, as the mycelia of mycorrhizal basidiomycetes must be abundant in the same habitat. However, bleaching of litter is generally considered to be a sign of basidiomycete activity (Hintikka, 1970; Chapter 13) and in some cases this is very obvious, as when large bleached patches are found beneath troops of fruit bodies of *Collybia peronata* in *Fagus* litter.

We know much less about the activities of basidiomycetes in the H-layer. None of the lines of evidence given above is very helpful with H-layer material, and isolation studies indicate a greatly increased rôle for heavy-sporing moulds such as *Trichoderma* and *Penicillium*. When F-layer material becomes H-layer material, the greater part of it has been eaten by small animals, and the litter has become essentially a mass of animal pellets. The initial unpalatability of fresh litter has been progressively lost in the F-layer stage. One cause of unpalatability is the presence in the original plant matter of phenolic compounds, which are more likely to occur in the litter of acid-loving plants, and on acidic, nutrient-poor, sites. Many workers, including Satchell and Lowe (1967) have shown that such compounds have a deterrent effect on detritus-feeding animals. Phenolics may be lost by simple leaching, but microbial activity is probably more important. As Lindeberg (1948) and others have shown, litter-inhabiting basidiomycetes are strong producers of polyphenol oxidases; in the long run this property may be responsible both for the bleaching of litter and also for its increased palatability.

Another factor related to palatability is the state of the nitrogen present. In mor litter, nitrogen is scarce anyway, and C:N ratios of around 100 are common. Many litter fungi, including basidiomycetes, can tolerate this condition, and produce mycelium with a much narrower ratio than the material that they feed on. For this reason, leaves permeated by mycelium should be more nutritious to soil animals than

Table 2. *The ability of various species of basidiomycete to decompose, in pure culture, synthetic complexes formed from protein (either gelatin or leaf protein from* Sambucus) *by reaction with phenolic-containing extracts from various plants.* The cultures were incubated for 7 months. (After Handley, 1954)

| | Source of phenolics | | | |
	Quercus	Pinus	Acer	Calluna
Collybia butyracea	++	++	++	++
Hirschioporus abietinus	++	++	++	++
Lenzites betulina	++	++	+	+
Coriolus versicolor	++	+	++	+
Collybia dryophila	Nt	+	++	Nt
Lentinus lepideus	Nt	0	++	Nt
Mycena pura	Nt	0	++	Nt

0 No change.
+ Complex partly decomposed.
++ Complex completely decomposed.
Nt Not tested.

raw litter. In addition, much of the nitrogen in mor litter is in the form of phenolic–protein complexes (Handley, 1954) which seem to be of low digestibility to animals. Handley studied the decomposition of these complexes by synthesising them in the laboratory and testing them with pure cultures; a small selection of his data appears in Table 2. Basidiomycetes, including wood decomposers and also litter fungi such as *Collybia butyracea*, were capable of decomposing the complexes produced from a variety of plant phenolics. Some of his assessments suggested that particular fungi were more active when the phenolics were derived from certain kinds of plant, so the compounds could exercise selectivity over fungal decomposers. This may be so, but the conditions of Handley's tests were too artificial for such conclusions to be properly drawn. Basidiomycetes have access here to a nitrogen source that seems to be closed to animals, and perhaps to some other micro-organisms as well.

The increase in palatability and reduction of C:N ratio, which occur during fungal decomposition of F-layer material, are the basic reason why a prolonged phase of basidiomycete decomposition comes to an end. When basidiomycetes have sufficiently permeated and altered the material, soil animals invade and destroy the substrate.

Not all basidiomycetes that fruit on the forest floor are decomposers. It is well known that typical mycorrhizal fungi, such as species of the

genera *Amanita* and *Boletus*, show negligible decomposing activity when cultures are incubated with litter materials. It is generally useful to think of decomposers and mycorrhizal fungi as being two watertight, mutually exclusive classes, both spreading their mycelium in the same material but essentially using it for different purposes: the decomposers as a source of energy, and the mycorrhiza-formers as a source of inorganic elements. The only really satisfactory evidence for a mycorrhizal rôle is the synthesis of mycorrhizas with seedlings in pure culture, and the only satisfactory evidence for decomposing ability is the incubation of pure cultures with sterile litter resulting in a significant loss of weight. In these ways, many species have now been claimed as one or the other, but many are still unclaimed – the smaller toadstools in the Entolomataceae, for instance, seem to be a largely uncharted group. Some higher fungi are probably active in both capacities. *Laccaria laccata* was shown by Mikola (1956) to be able to decompose litter in pure culture, while several authors, including Suggs & Grand (1972), have demonstrated mycorrhiza formation with various trees. Since several genera of agarics contain both mycorrhiza-formers and decomposers, it seems possible for a fungus to evolve from one way of life to the other, and one should reasonably expect to find some species with both capacities; indeed Lyr (1963) showed that some typical mycorrhizal fungi like *Amanita citrina* and *Suillus variegatus* produced small yields of cellulase and xylanase, and could play a small part in the destruction of litter materials.

Decomposition studies with pure cultures

By pure-culture methods, quite a long list of species have been shown to be litter-decomposers – most of these are in the genera *Mycena, Marasmius, Collybia* and *Clitocybe* (Lindeberg, 1944, 1947; Hering, 1967). This confirms the impression given by these species in the forest, where they are associated with local patches of bleaching of mor litter, and mycelium can be followed out from the toadstool to pieces of decomposing leaf. On similar grounds, I think that others, including certainly species of *Psathyrella* and *Tubaria*, are likely to be litter-decomposers, but there has been no laboratory study of them. This kind of evidence cannot be gained easily in mull, where the mycelial connections of both mycorrhiza-formers and presumed decomposers are less obvious than in the organic horizons of a mor. Watling (Chapter 1) discusses in detail possible ecological groupings of basidiomycete taxa.

Figure 1 shows some results from a pure-culture decomposition study on *Quercus* litter. The two basidiomycetes tested caused substantially greater dry-weight losses than the non-basidial litter fungi; moreover, they showed every sign that these rates could be maintained over long periods, whereas moulds like *Trichoderma viride* gave an early flush of decomposition and sporing and then stagnated. Similar results were obtained in a study by de Boois (1976). Assuming an exponential rate of dry-weight loss, Hering's (1967) data gave an estimate of the half-life of litter decomposed by *Mycena galopus* of about 600 days (or $-$ 0.1% day^{-1}). This estimate was made at temperatures approximating to mean annual outdoor temperatures (12–15 °C). Higher temperatures give increased rates, and Lindeberg (1947), with *Fagus* litter incubated at 25 °C, obtained data which yielded estimates of 200–250 days (approx. $-$ 0.3% day^{-1}) for this and several other species.

Much the greater part of the dry matter of litter is in the form of cell-wall macromolecules; estimates of the percentage dry matter made up by lignin, cellulose and hemicellulose vary from 70% to over 80%. Virtually all the basidiomycetes studied by Lindeberg were able to decompose lignin as well as cellulose and hemicellulose, so they were physiologically akin to the white-rot fungi of wood. Most of them caused bleaching of the litter in pure culture, and this effect may be correlated with lignin-decomposing ability, as it is among wood-rotting fungi
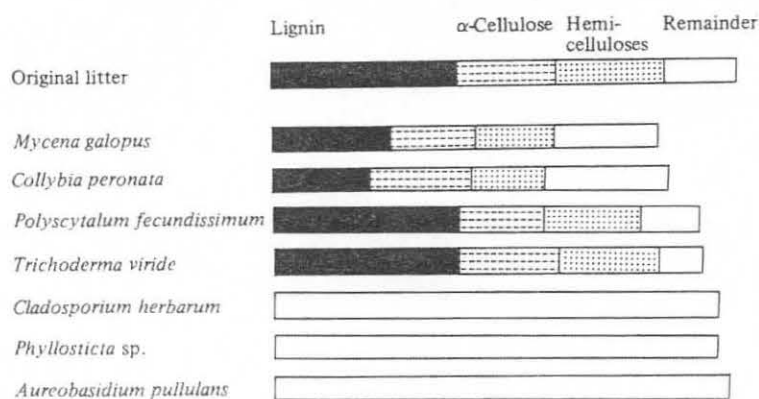

Fig. 1. Changes in dry weight and chemical composition of sterilised *Quercus* leaf litter incubated with single cultures of fungi for 6 months at 12–15 °C. For the last three species, only dry-weight changes are given. Data from Hering (1967).

(Davidson, Campbell & Blaisdell, 1938). It was very common to find that lignin disappears from the litter faster than cellulose. The very small degradation of cellulose by *Collybia peronata* in Fig. 1 confirmed similar results obtained with this fungus by both Lindeberg (1944) and Harris (1945). There is every reason to think that basidiomycetes are the main agents of lignin destruction in mor litter, but it is probably premature to claim, as is sometimes done, that they are the sole agents. Most claims for the involvement of other kinds of micro-organisms are based on tests with 'extracted lignin', and may be unreliable as a guide to what occurs in nature. Where intact forest litter has been incubated with pure cultures, lignin decomposition has been convincingly recorded only with basidiomycetes, though Haider & Schetters (1967) demonstrated losses of lignin in straw, caused by imperfect fungi that were probably non-basidiomycetes. There is still some doubt about basidiomycetes that do not bleach litter – are they lignin-decomposers or not? Mikola (1956) recorded that *Laccaria laccata* was one such fungus but did not carry out chemical analyses of litter. Chastukhin (1962) also found a non-bleaching type of decay with *Lepiota procera*; however, Lindeberg (1947) did find that this species degraded lignin.

Studies in glass flasks do not, of course, indicate how much decomposition is carried out in nature by the same species, when competing with other decomposers. Interesting data (Fig. 2) were obtained by Saitô (1957), who studied the weight changes in *Fagus* leaves undergoing a bleaching type of decay on the forest floor, almost certainly caused by basidiomycetes. The chemical changes were similar to those
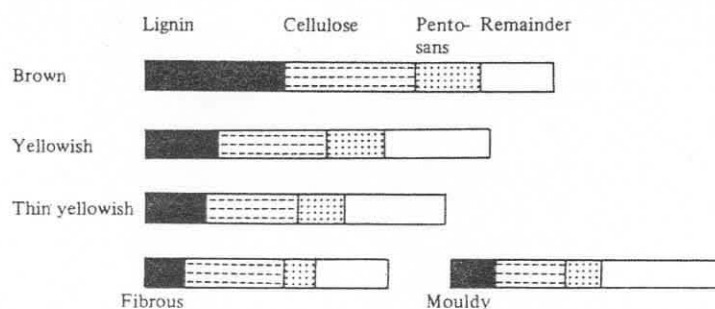
Fig. 2. Changes in dry weight and chemical composition of *Fagus* leaves undergoing a bleaching type of decomposition in a Japanese forest. Dry-weight changes from leaf-area measurements on weighed samples. The terms 'brown', etc. denote successive layers in the soil profile. Data from Saitô (1957).

occurring in pure-culture tests, with lignin disappearing faster than cellulose. The leaves had lost 30–40% of their initial dry weight by the time they reached the condition described by Saitô as 'fibrous' or 'mouldy'; both these terms probably indicated the end of an exclusive basidiomycete phase, with massive invasion by animals and non-basidiomycete fungi. In pure-culture studies these competitors are kept out, and much higher weight losses can be found with basidiomycetes alone. Chastukhin (1962) carried out prolonged incubations, and took account of the fact that in glass flasks the salts released by decomposition cannot escape, and will accumulate until they become toxic. His samples were washed in sterile water, removing both salts and soluble organic matter. Several species caused dry-weight losses of over 70% in two years (82% with *Collybia dryophila*). This work suggested that these fungi were able to destroy all kinds of macromolecule present in litter; however, in nature the substrate is usually eaten by soil animals when less than half of the dry matter has been lost.

Pure-culture studies show that fungi that bleach litter also acidify it; the white rots of litter seem to differ from those of wood in this respect. In studies on *Mycena galopus* (Hering, 1967) there was a fall of pH in 6 months from 4.0 to 3.2, and similar changes were recorded for many fungi by Mikola and Lindeberg. The fall in pH may bring an ecological advantage, since the fungus generates soluble compounds, including sugars, by hydrolysis, and a low pH probably has the effect of restricting bacterial exploitation of these compounds. Kühnelt (1963) pointed out that litter bleached and acidified by the activity of *Clitocybe infundibuliformis* was very poor in most kinds of soil animals, although a few species preferred it. By delaying animal attack, such effects may help to prolong the survival of the fungus.

The experience of collectors shows that most species of decomposer basidiomycetes are relatively specific to certain kinds of litter. For example, *Collybia dryophila* prefers broad-leaved litter, and *Marasmius androsaceus* prefers conifer needles. Little is known of any biochemical background to such differences. In a few cases, such as *Marasmius hudsonii* which is strictly limited to leaves of *Ilex aquifolium*, it may well be that the fungus is partly parasitic, colonising the leaves before they reach the ground. But in pure cultures many species do not show strong preferences, as Table 3, from Mikola (1956), shows. All the fungi he tested decayed *Populus tremula* litter about twice as fast as *Pinus* needles; this was equally true of the needle-fungus, *M. androsaceus*. Likewise, there seemed to be no chemical factor in pine needles to

Table 3. *Percentage weight losses in sterilised samples of leaf litter incubated with basidiomycetes for 107 days.* (From Mikola, 1956)

	Pinus needles	Populus leaves
Collybia dryophila	17.2	46.3
Micromphale perforans	15.0	25.8
Mycena galopus	14.7	27.0
Collybia confluens	14.0	19.2
Marasmius androsaceus	13.4	31.8
Laccaria laccata	5.9	13.2

prevent attack by *Collybia dryophila*, nor even to slow its growth detectably. In nature, when *M. androsaceus* grows on mixed leaves and needles, fruit bodies can sometimes be found attached to *Quercus* leaves, but it does not seem to be able to maintain itself indefinitely on purely broad-leaved litter. The natural distribution of the various species probably reflects the result of long-continued competition between species.

We thus have a reasonable, if partial, picture of the activities of decomposer basidiomycetes growing on litter. We can also make rough estimates of the amount of decomposition that they carry out on the litter. For Scandinavian forests, an estimate can be gained from the work of Hintikka (1970) who coined the term 'white-rot humus' for a material predominantly attacked by basidiomycetes (see Hintikka; Chapter 13). Coverage of the forest floor by this humus varied from low levels to about 10% of the litter present. As an estimate of basidiomycete involvement, this is subject to at least two qualifications. Firstly, the total throughput of the bleaching process may be greater than the proportion of bleached litter visible at any one time. Secondly, some basidiomycete species cause little bleaching in the forest. We can certainly expect decomposer basidiomycetes to make a significant contribution wherever they occur, and they do occur very widely.

Fruiting as an index of activity

We can make the last statement of the previous section confidently because of the occurrence of fruit bodies. They are useful indicators of the complement of species present, and of the distribution of a given species across a site. Counts or weighings of fruit bodies,

however, can never be better than a rough guide to the relative importance of the various species. The production of fruit bodies never utilises more than a small fraction of the energy contained in the litter that gives rise to them. For comparison, one should consider that 100 kg of fresh mushroom compost (including water) can yield something of the order of 25 kg of mushrooms within 8 weeks (Atkins, 1974). Taking a whole year's harvest, the equivalent yield from 100 kg of woodland litter seems to be at best 0.2–0.5 kg, i.e. of the order of a hundred times less. This disparity would not be greatly different if dry-weight figures were used. If mycorrhizal species were included, the yield of the forest floor would be much higher, but these species are drawing on carbon sources not included in the litter fall. It seems probable that decomposer basidiomycetes assimilate far more carbon than they ever use in producing fruit bodies; the main reason for this may be the limitation on fruiting imposed by the weather.

Fruiting behaviour is probably not a good guide to the period of activity of the fungus; in Britain, strands and apparently actively growing basidiomycete mycelium may be found at any time of the year, but, in general, fruiting of soil and litter types is restricted to the summer and autumn. Figure 3 shows the seasonal fruiting profiles of
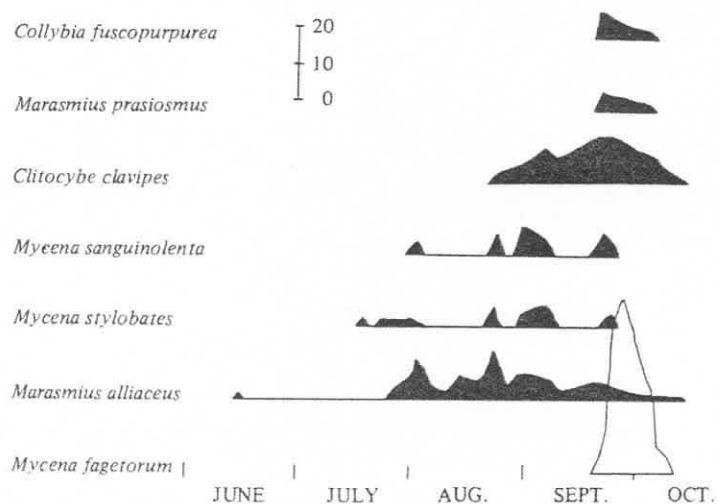

Fig. 3. Numbers of fruit bodies of some decomposer agarics, recorded every 2–3 days during the fruiting season in a plot of 400 m² in a *Fagus* forest at Rabsztyn, Poland. Data from Guminska (1962).

some decomposers in a Polish woodland of *Fagus* (Guminska, 1962). Three of the species showed a series of peaks and troughs of fruiting in response to the weather; the effect of a wet spell followed by a dry one in late August can be clearly seen. These decomposers probably resemble the cultivated mushroom, in that they can fruit at any time of the year, given a suitable temperature and soil moisture. As their fruit bodies are small, forming primordia at relatively shallow depths, they are markedly affected by fluctuations in moisture, while the large *Clitocybe clavipes*, arising deeper, is less affected. Its seasonal curve resembles that shown by many mycorrhizal fungi. Three other species, typified by *Mycena fagetorum*, were limited to an autumn season regardless of the weather. Several of the *Mycena* species studied by Hintikka (1963) over five successive seasons showed a similar limitation (Fig. 4). This could represent a biological advantage for these fungi, since, in autumn, conditions are damper, permitting the easier establishment of new colonies from spores, which may also be able to colonise the current year's litter, before or after it falls. It seems that this group of decomposers is 'taking a cue' for fruiting from some feature of the environment, such as frosts or changes in daylength. For the present we can only guess at the nature of this cue, which needs to be explored experimentally.

We have, from observation and experiment, ample evidence to confirm what was said about litter-decomposing basidiomycetes in the opening sentence – their rôle is a very important one. In forests, they
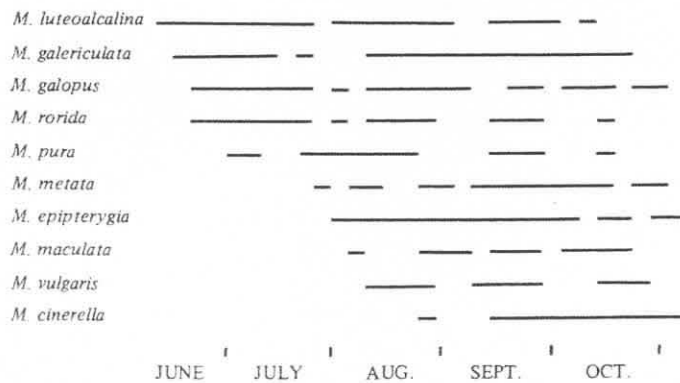
Fig. 4. Fruiting of *Mycena* species on the forest floor in Finland. The lines show 5-day periods during which the given species was found fruiting at least once during 5 years of observations. Data from Hintikka (1963).

are almost ubiquitous; when tested, they decompose litter materials at a steady rate over long periods, and they seem to make a vigorous attack upon some compounds, such as lignin, that would decompose slowly or not at all in their absence. A great deal more remains to be learned about their rôle, and about the specific attributes that cause a given species to be confined to certain materials or to certain soils. To put the present state of our knowledge into proportion, one should realise that only about fifty species of litter-decomposing basidiomycetes have ever been subject to any sort of experimental investigation, while the number of non-mycorrhizal basidiomycete species in the forest floor, in Britain alone, is probably in excess of 500.

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